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XL.—*Notes on the Madreporarian Genus Astræopora, as represented by the Specimens in the British Museum (Natural History).* By H. M. BERNARD, M.A. Cantab., F.L.S., F.Z.S.

[Plate XIV.]

THE genus *Astræopora* was founded by de Blainville in 1830* to contain specimens selected from Lamarck's genus *Astræa*. In working over the same ground again for the publication (in 1836) of his 'Manuel d'Actinologie' de Blainville transferred one of his species of *Astræopora* to his genus *Gemmipora* (*Turbinaria*). This apparently suggested to him the possible close affinity between the two genera. Dana† accepted this affinity, but with a note of interrogation; he evidently took it on authority, and in spite of its inconsistency with his principles of classification according to the methods of budding. The budding of *Gemmipora* he described as inferior, a description which could not certainly apply to that of *Astræopora*; hence his hesitation. No such grounds for hesitation existed in the system of Milne-Edwards and Haime, and the two genera were definitely classed together by these authors in a subfamily Turbinariinæ, first in 1851‡, and then by Milne-Edwards in the third volume of 'Les Coralliaires.' This classification has persisted ever since, being accepted by

* Dict. des Sciences Naturelles, t. lx. p. 348.

† 'Zoophytes,' p. 115.

‡ Les Polyp. foss. d. Terr. palæozoïques, p. 141.

Martin Duncan * in his revision of Milne-Edwards's system in 1884.

This definite association of *Astræopora* with *Turbinaria* as members of the same subfamily led to the recognition of an important generic distinction. *Turbinaria* was distinguished from *Astræopora* by its well-developed columella. This led again to the transference of another of de Blainville's *Astræopora*s to the *Turbinarians*; *Astræopora stellulata*, possessing a columella, became *Turbinaria stellulata*, and has since been looked upon as a transition form connecting the two genera. My own study of the specimens of the two genera contained in the British Museum collection has led me to the conclusion that there is no close affinity between them. They are independent developments of cœnenchymatous corals, their respective specializations being too distinct to be deducible one from the other.

I desire again to tender my sincerest thanks to Dr. Günther, F.R.S., the Keeper of the Zoological Department of the Museum, for the kindly interest he has taken in my work, and to Professor Bell for his readiness to assist me in every way.

There are thirty specimens of *Astræopora* in the National Collection, this small number being probably indicative of the rarity of the genus. In his recent visit to the west coast of Australia, Mr. Saville Kent only succeeded in obtaining a single specimen. These thirty specimens fall into fourteen groups, sufficiently distinct to rank as species. The number of species hitherto recorded is only five; hence there are at least nine new species represented in the collection.

Three of the five recorded species were established by Lamarck. His descriptions are very short and inadequate, and their identification is at once difficult and uncertain. Of the other two recorded species the single (type) specimen of one (*A. expansa*, Brüggemann †) was fortunately in the collection, and four figures of the other (*A. profunda*, Verrill) are given by Dana ‡ in the Atlas to his 'Zoophytes' under the title of *A. pulvinaria*, Lamarck.

Accepting Lamarck's suggestion that two of his species—*A. myriophthalma* and *A. pulvinaria*—might be different growths of the same, the established species were reduced to four, and the thirty specimens belonging to the Museum were ultimately arranged into fourteen species, ten of which are new.

* 'Journal of the Linnean Society,' Zoology, vol. xviii. (1885).

† Described in Ann. & Mag. Nat. Hist. (4) vol. xix. p. 416 (1877).

‡ Plate xxix. figs. 3, 3a, 3b, 3c.

Earliest known Stage.—The youngest colony discovered (on the dead portion of a larger specimen*) is a minute plate-like growth of cœnenchymatous reticulum, not quite 3 millim. in longest diameter. There is a central calicle (the parent calicle of the colony), readily distinguishable by its size, and an irregular ring of smaller (daughter) calicles. The whole is contained in a saucer-like epitheca, with edges bent up all round free of the substratum. The colony has apparently grown unsymmetrically; instead of being a complete circle, the corallum has spread out symmetrically only on one side of the parent calicle, as shown in the figure (Pl. XIV. fig. 1). There are two cycles of septa, the first being conspicuous. The daughter calicles develop in the cœnenchyma, and one (*a*) is seen at the extreme edge of the colony, part of its wall being formed by the epitheca. There is no connexion between the calicles other than the canal-system of the cœnenchyma. The typical structure of the cœnenchyma is not visible at this stage; it can only be detected in the larger specimens.

Later Developments.—Comparison of adult specimens showed that there are at least three fairly distinct methods of growth, according to which such an initial colony as that just described may develop further. I have therefore divided the genus primarily according to the methods of growth.

First Method of Growth: Explanate.—The corallum expands chiefly laterally, the growth in thickness being slow and irregular. The epitheca continues to grow and to support the edge of the corallum. The most perfect example of this is Brüggemann's species *Astræopora expansa*†, which is purely explanate, the thin expanding edges rising freely but gradually from the substratum, accompanied and supported by a well-developed concentrically wrinkled epitheca. The calicles are far apart and for some distance from the edge appear, on being held up against the light, to penetrate right down to the epitheca.

Another but less perfect example is Lamarck's *myriophthalma*, which forms large plates; these, when young, may be thin and flat, but when old become irregular and humpy, ultimately forming great mounds as successive growths creep over their uneven predecessors. There is in the collection a good series showing these changes; but for the presence of the intermediate growths the oldest and youngest specimens would almost certainly be classed as distinct species.

In this and other explanate forms the relation between the epitheca and the expanding edges is of considerable interest.

* The registered number of which is 91.3.6.34.

† Ann. & Mag. Nat. Hist. (4) vol. xix. p. 416.

Where the epitheca follows the growing edge closely, the latter tends to grow upwards free of the substratum, but where the epitheca lags behind the growing edge, the latter tends either to droop, which is the more usual, or (*A. myriophthalma*) to send down long pendent and twisted calicular tubes, which are gradually enveloped and closed by the advancing epitheca. It is obvious that this explanate growth may merely creep over the substratum as a simple incrusting corallum.

I have distinguished in all five explanate species, three of which are new.

Second Method of Growth: Pulvinate.—The growth is in this case chiefly in thickness. The calicles grow rapidly in length, tabulæ being developed at intervals, as is the case in the lengthening calicles of glomerate Turbinarians. New calicles appear for a time at the expanding edges of the corallum, and others between the lengthening calicles as they diverge (fig. 2). In time the lower portions of the stock die, and no new calicles are added round the edge of the original epitheca (*e'*). The living top, on the other hand, goes on expanding by the continued divergence of the calicles and the addition of new ones between the old. This uppermost living layer tends to hang down over the old dead portions, in which case a new (secondary) epitheca (*e''*) appears, restraining the downward growth of the edges. As layer succeeds layer, enormous top-heavy bolster- or cushion-shaped masses are produced. The top-heaviness is obviously due to the fact that the early death of the lower portions limits the size of the base.

Sooner or later such masses break off and roll over. The living layer will then be confined to the uppermost portion of the overturned stock, on which it soon forms another great top-heavy mass (see fig. 3, in which *a* is the original upper surface of an overturned stock).

Among the specimens in the collection are several showing this method of growth. There is a complete series from Tongatabu, which I have named *A. Listeri*, after Mr. J. J. Lister, who generously presented them to the Museum. Fig. 3 represents the largest specimen, forming a great mushroom-like mass 7 inches in diameter.

Many of the other specimens which I attribute to this method of growth are unfortunately only fragments. All these fragments, however, show enormously long calicles with tabulæ, and, further, the living ends of the calicles bend outwards and form at the edge an overhanging margin such as that shown in the diagram fig. 2. These growths are thus obviously not explanate, nor are they globular. As far

as it is possible to judge from a fragment, everything points to their growth being of the type described.

I have arranged five new species under this division. The only specimen previously named is one of Dr. Klunzinger's "*A. myriophthalma*" from Koseir. It is unfortunately only a fragment, but it shows all the features just mentioned and has an overhanging edge. It could hardly, therefore, belong to the explanate forms. In Dr. Klunzinger's original description* we read of the coral as being incrusting, $1\frac{1}{2}$ centim. thick; but the greater number of the specimens gathered were massive, 6–8 centim., with "incrusting edges." This at first sight looks as if the same species may adopt either the explanate or the pulvinate type of growth. This assumption is, however, not necessary; overturned blocks are grown over by the living layer in such a way as entirely to justify the term "incrusting." On the whole, therefore, Dr. Klunzinger's description is quite consistent with the interpretation of the species here given. Besides, I was compelled to give Dr. Klunzinger's specimen another name, having identified several large, flat, humpy specimens as the true *myriophthalma* of Lamarck. The new name, "*A. Ehrenbergi*," is based upon Dr. Klunzinger's discovery that his specimens are specifically identical with Ehrenberg's (*Madrepora*) *Phyllopora sphaerostoma* et *leptostoma*†.

The name "pulvinate," or cushion-shaped, given to this type of growth was suggested by Lamarck's species "*pulvinaria*," which, being only a different growth of *A. myriophthalma*, does not really belong here; but having once temporarily arranged it under this heading, I felt at liberty to retain the name for this division, especially as the species "*pulvinaria*," being suppressed, could lead to no confusion.

Third Method of Growth: Globular.—This form appears to be due to the great lengthening of the calicles, accompanied by the rolling of the cœnenchymatous skeleton over the edge of the epitheca. The earliest stages I have unfortunately not seen; but examination of the available specimens leaves little doubt that this is what really takes place. The globes thus formed often appear to be free, and may have started on a projection or loose portion of the substratum. New layers cover the old, so that the mass is in time composed of a system of concentric shells, the upper one alone living (fig. 4). As in the glomerate Turbinarians, each new growth seems to start from the summit of the globe and to creep down all

* 'Die Korallenthier des rothen Meeres,' Th. ii. p. 53 (1879).

† 'Beiträge zur Kenntniss d. Korallenthier des rothen Meeres,' 1836, p. 114.

round. The advancing edge is generally restrained by an epitheca, which may form a regular pocket-like fold, even covering up the calicles. The coenenchyma may, however, roll over this fold and continue to descend (figs. 4 and 5a).

These balls are sometimes overturned, in which case what was the former under-surface is grown over; Lamarck describes his specimen of *A. punctifera* as being like a cannon-ball without any scar of attachment. The single specimen in the National Collection, which I have identified with Lamarck's species, shows that the innermost ball (1) round which the recent growths have crept had been rolled over (fig. 5).

The difficulty of ascertaining the exact method of development of the globular growth is increased by the fact that the dead coral of the older central portions is very often hollowed out by boring mollusks. There is, however, in the collection a young specimen (too young to name) closely investing a dead and corroded fragment of some branched coral. This may perhaps be the nucleus of a globular form.

There are, again, other single specimens which appear as if they might belong as well to the pulvinate as to the globular growth; without further material their true position can only be guessed. While the pulvinate method of growth is quite distinct from the globular, it is possible that there is another form of growth connecting the two.

There were in all four different species showing this method of growth, of which two are new*.

The Calicles.—The calicles are chiefly remarkable for their great depth and for the feeble development of the septa, which may be present in as many as three cycles. The primaries alone project towards the centre as thin lamellæ, and generally only far down in the fossa. The third cycle seldom consists of more than fine ridges at the margin, extending but a short way down the fossa.

As in the glomerate Turbinarians, the calicles form tabulæ when, in the pulvinate method of growth, they have to lengthen.

The chief characters of taxonomic value presented by the calicles are their average size, their distance from one another, the fine structure of their margins, and, when protuberant, the character of the protuberance—hemispherical, conical, or papilliform.

* Martin Duncan (Mem. Geol. Survey India, ser. xiv. p. 99, pl. xxv. fig. 6) has described a fossil Astræoporan from Sind, *A. hemispherica*. The base was covered with epitheca and the corallites shallow (?). This appears to have belonged to this type of growth.

The Cœnenchyma.—The most characteristic feature of the genus is afforded by the cœnenchyma. It is constructed of two elements—the costæ, which, instead of being lamellate, break up into long tapering echinulæ (fig. 6). The echinulæ all bend upwards and are united with one another by regular, nearly horizontal floors, for the support of which the echinulæ act as pillars. These are thick near the polyp-cavities, but thin halfway between them. The synapticular floors are, at least in the uppermost layers, perforated by large round holes.

The different appearances presented by the coralla is largely due to the respective developments of these two elements. When, as in cases of rapid growth in thickness, the costal elements are most developed, the surface is highly echinulate. The synapticular floors, on the other hand, are then often feebly developed. Again, in cases of explanate growth, the echinulæ may be feebly developed and the horizontal floors strongly developed. Dana proposed to divide the genus into two groups (which might “constitute different genera”) according to this distinction. But no such division would be admissible; the structure is essentially the same.

Other variations in the cœnenchyma are due to irregularities in the growth of the two elements, so that the texture may here and there appear confusedly reticulate, or foliate, or (by the thickening and nodulation of the elements) granular.

On the Relation of Astræopora to Turbinaria.—In my recent paper in this Magazine* on the latter genus I suggested that it was possible that *Astræopora* represented a more primitive cœnenchymatous coral than either *Madrepora* or *Turbinaria*. *Madrepora* could perhaps be deduced from a simple incrusting form like *Astræopora* by the special growth and lateral budding of some of the corallites, while, again, *Turbinaria* might be deduced from *Madrepora* by the further specialization of this lateral budding. The following are the chief reasons which make me now think it highly improbable that *Astræopora* has any close affinity with *Turbinaria*:—

(a) The epitheca in *Astræopora* persists and plays an important part in the development of the corallum. As we have seen, the earliest buds develop round the parent polyp contained within a common saucer-like epitheca. This epitheca follows and more or less supports the edges of the expanding corallum.

* Ser. 6, vol. xv. June 1895, p. 499.

When the corallum grows in thickness and the basal portions die, a secondary epitheca appears under the edges of the living layer as it creeps over the older dead portions. In *Turbinaria* the earliest buds arise from the parent polyp above and free from the epitheca, which merely spreads out as a cementing substance beneath the expanding base or foot of the cup-shaped corallum. But here again also a secondary epitheca, which can have no connexion with the original epitheca, may develop under flat horizontally expanding leaves and under the edges of incrusting glomerate forms. The two genera, however, rise up so very differently from their respective epithecæ that there are no grounds for attempting to deduce one from the other.

(b) The cœnenchyma in *Astræopora* is far more highly specialized than it is in *Turbinaria*.

(c) In *Turbinaria* the intracalicular portions of the septa are, as a rule, highly developed, uniting at the base of the fossa to form the conspicuous columella. The extracalicular portions show no special development, but merely form the cœnenchyma connecting the polyps. In *Astræopora* the intracalicular portions of the septa are very feebly developed, only the first cycle even approaching the centre. As each polyp advances in age and length, the new cycles, second and third, are less and less developed. On the other hand, the extracalicular or costal portions of the septa are highly specialized, forming the characteristic cœnenchyma of the genus.

While both genera therefore are cœnenchymatous corals, *i. e.* in both the whole corallum which rises freely above the epitheca is a product of the septa, and *may* be related, we have no evidence to support such relationship; indeed, they differ from one another as far almost as such corals could differ, from the very outset of their respective life-histories.

Parasites and Commensal Annelids.—It is worth noting that the Balanids which infest some of the highly echinulate *Astræoporans* defend themselves from being overgrown by the cœnenchyma by formidable series of spikes on their shells, which closely resemble in size the echinulæ of their hosts. The Balanids infesting the *Turbinarians* with their less echinulate cœnenchyma are defended by a much less pronounced arrangement of teeth.

There are several records of commensal Annelids whose calcareous tubes are worked up with the skeletal formations of corals. The most remarkable case, perhaps, is that of

*Heliopora cærulea**, in which the tubes of the Annelids are more numerous than the polyp-cavities, and must exercise a powerful influence on the growth of the corallum.

Among the *Astræoporans* I have found two cases. One is a single specimen (*A. Kenti*, sp. n.) discovered by Mr. Saville Kent on the west coast of Australia, in which only a few tubes were present, and appeared somewhat to disturb the coral. The other (*A. gracilis*, sp. n.) is from the Solomon Islands, and was discovered by Dr. Guppy. In this case the worm-tubes interlace with the long polyp-cavities, and open on the surface in great numbers, both coral and worm being apparently adapted to one another. The tubes are often pink, and even red, in colour, and much larger than those found in *Heliopora*, ca. $\frac{3}{4}$ millim. in diameter, as compared with ca. $\frac{1}{4}$ millim.

EXPLANATION OF PLATE XIV.

- Fig. 1.* The youngest specimen found, consisting of a parent-polyp (*pc*), with a group of daughter-polyps developed chiefly on one side, the whole corallum contained in a saucer-like epitheca (*e*). The daughter-polyp (*a*) is developing in contact with the epitheca, which forms part of its wall.
- Fig. 2.* Diagram to explain the pulvinate method of growth. The corallum rises from the original epitheca *e'*, the corallites lengthening greatly in the middle. As the lower parts die, the top expands as shown; under the edge of the overhanging top a secondary epitheca, *e''*, develops, and appears to restrain the downward flow.
- Fig. 3.* Largest specimen, showing the pulvinate type of growth, developed on the edge of a dead overturned previous growth. *a*, the former top of the dead growth.
- Fig. 4.* Diagram illustrating the globular method of growth. The original youngest growth is hollowed out by boring mollusks. *e'*, the edges of the original epitheca; *e''*, *e'''*, *e^{iv}*, folds of secondary epitheca which have restrained the downward flow of the living layers. At *a* the living layer is beginning to roll over the epithecal fold.
- Fig. 5.* Specimen of *Astræopora punctifera*, Lamarek, showing four layers. The first (I) has been overturned; its corroded upper face is seen in the plane of the paper; at *a* the cœnenchyma is rolling over the epitheca.
- Fig. 6.* Typical structure of the cœnenchyma (from *A. Ehrenbergii*, = *A. myriophthalma*, Klunzinger, non Lamarek). The synapticular floors form nearly regular tiers, supported by tapering costal echinulæ.

* Cf. Moseley, Phil. Trans. vol. clxvi. pt 1, 1876, p. 96, and Saville Kent's 'Great Barrier Reef,' pp. 192-194; also, for the case of *Mycedium fragile*, cf. Fewkes, 'American Naturalist,' vol. xvii. p. 595 (1883).